

Habitat Fragmentation and the Persistence of Lynx Populations in Washington State

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ABSTRACT Lynx (*Lynx canadensis*) occur in the northern counties of Washington state, USA; however, current distribution and status of lynx in Washington is poorly understood. During winters 2002–2004 we snow-tracked lynx for 155 km within a 211-km² area in northern Washington, to develop a model of lynx–habitat relationships that we could use to assess their potential distribution and status in the state. We recorded movements and behaviors of lynx with a Global Positioning System and overlaid digitized lynx trails on various habitat layers using a Geographic Information System. Based on univariate analyses, lynx preferred Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests, with moderate canopy and understory cover, and elevations ranging from 1,525 m to 1,829 m but avoided Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forests, openings, recent burns, open canopy and understory cover, and steep slopes. A map of suitable lynx habitat based on a logistic regression model built using these candidate variables revealed that habitats at elevations >1,400 m where lynx historically occurred in Washington are intersected and fragmented by landscape features and forest conditions that are generally avoided by lynx. Our habitat suitability map predicts 3,800 km² of lynx habitat in Washington that could support 87 lynx, far fewer than previous estimates. Since 1985, natural fires have burned >1,000 km² of forested habitat in Okanogan County, the only region in Washington where lynx occurrence has been documented during that period. Loss of suitable habitat from natural and human-caused disturbances, and the lack of verifiable evidence of lynx occurrence in historic lynx range, suggests that fragmented landscape conditions may have impeded recolonization of these areas by lynx. Consequently, translocations may be necessary to ensure lynx persistence in Washington. We suggest that managers assess the potential for translocation by first identifying the scale and distribution of potential foraging habitats for lynx based on our or similar habitat models, survey various habitat conditions to obtain reliable estimates of snowshoe hare densities, and identify a genetically compatible source population of lynx. If habitat and source populations are adequate, reintroducing lynx to areas of their historic range may be an appropriate conservation strategy. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1518–1524; 2008)

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In 1993, the Washington Department of Fish and Wildlife listed the lynx (*Lynx canadensis*) as a State Threatened species (Stinson 2001); in 2000, lynx populations throughout the contiguous United States were classified as Threatened under the federal Endangered Species Act (U.S. Fish and Wildlife Service 2000). Based on museum specimens and other verifiable records, lynx populations have persisted in northern Washington, USA, since the late 1800s (McKelvey et al. 2000a, Stinson 2001; G. M. Koehler, Washington Department of Fish and Wildlife, and K. B. Aubry, United States Forest Service, unpublished data). In Washington, potential lynx habitat occurs primarily in the counties of northern Washington that are located on or near the southern border of British Columbia, Canada.

Telemetry studies conducted during the 1980s in the Cascade Range of northern Washington found lynx primarily in forests dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), or lodgepole pine (*Pinus contorta*), on mild to moderate slopes, and at

elevations >1,400 m (Koehler 1990; J. D. Brittell, Washington Department of Fish and Wildlife, unpublished report). Based on these forest-type and physiographic characteristics, available habitat for lynx in Washington was estimated at 9,555–12,579 km² (Washington Department of Wildlife 1993, Stinson 2001). McKelvey et al. (2000a) compiled both anecdotal and verifiable lynx occurrence records from throughout the contiguous United States and estimated 15,100 km² of primary lynx range in Washington. Potential habitat for lynx and intermittent observations of lynx and their tracks have been documented for the northeastern counties of Washington from the eastern slope of the Cascade Range in Okanogan and Chelan counties eastward to the Idaho border (Fig. 1). Based on these range estimates, the state wildlife agency estimated there were 96–238 lynx in Washington (Washington Department of Wildlife 1993, Stinson 2001).

Since these estimates of lynx numbers and potential habitat were published, we have identified additional insights on habitat-use patterns by lynx and snowshoe hares (*Lepus americanus*). The potential for substantial changes in amount of suitable lynx habitat due to recent stand-

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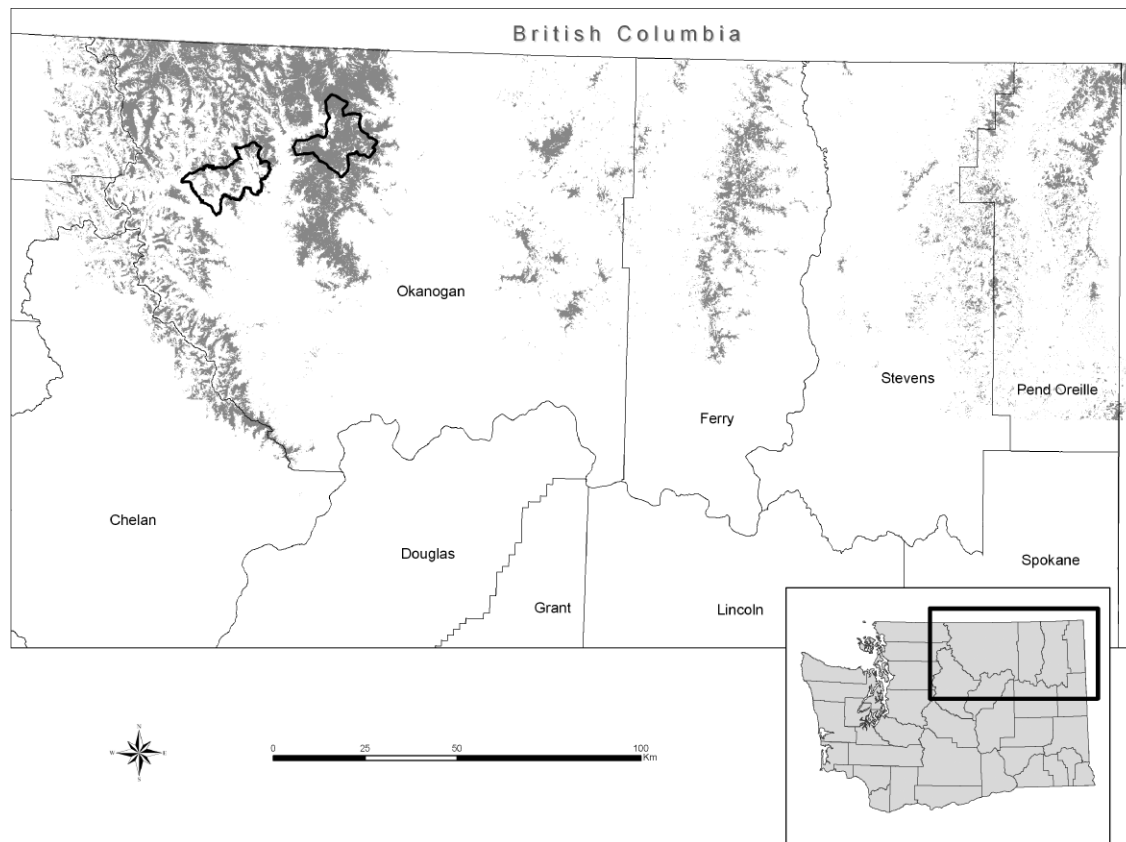


Figure 1. Extent of lynx habitat composed of Engelmann spruce and subalpine fir forest with canopy cover 11–39%, elevations ranging from 1,525 m to 1,828 m, and slopes $<30^\circ$ in northern Washington, USA, 2002–2004. The Black Pine Basin (W) and Meadows (E) study areas are shown in black outline.

replacement fires and insect outbreaks indicated the need to re-evaluate the status of lynx populations and available habitat conditions in Washington. From 2000 to 2004, von Kienast (2003) and Maletzke (2004) investigated habitat selection by lynx in the northeastern Cascade Range in Washington, and Walker (2005) conducted concurrent studies of snowshoe hare populations. We used information from these studies to develop a Geographic Information System (GIS) model of potential habitat for lynx in northern Washington. Our objectives were to evaluate the current extent of potential habitat for lynx in Washington, identify potential threats, and evaluate management actions that may help to ensure the persistence of lynx populations in Washington.

STUDY AREA

We studied habitat selection by lynx during the winters of 2002–2003 and 2003–2004 on a 211-km² study area in the Black Pine Basin on the Okanogan–Wenatchee National Forest in northern Washington (48°N 121°E). We selected the Black Pine Basin because of the historic presence of lynx, varied forest vegetation and elevations, and density of gravel roads (1.8 km/km²) that allowed for snowmobile access. Elevations ranged from 643 m to 2,134 m, with higher elevations (1,524–2,134 m) comprised of lodgepole pine, Engelmann spruce, and subalpine fir forests (55% of study area). Douglas-fir (*Pseudotsuga menziesii*) and ponder-

osa pine (*Pinus ponderosa*) forests dominated southerly aspects and comprised 37% of the study area. Openings comprised 2% and areas burned by wild fires and devoid of overstory comprised 6% of the study area. Shrub-steppe habitats dominated elevations $<1,066$ m and valley bottoms. Temperatures ranged from -26° C to 38° C (Western Regional Climate Center, Reno, NV, USA) and average annual snowfall was 315 cm at 655 m elevation.

METHODS

To investigate habitat selection by lynx, we followed lynx trails on snowshoes. To avoid influencing lynx behavior, we backtracked lynx trails if they were <24 hours old and forward-tracked them if they were >24 hours old. We first identified 6 39-km² search zones that approximated the average size of a female lynx home range (Koehler 1990). We used these zones to disperse our search effort and maximize opportunities for locating tracks of different individuals and to obtain a representative sample in both time and space during each winter. We randomly selected a unit from 4 9-km² search units that we established in each zone to begin systematic searches for lynx tracks. We surveyed a new zone each day and randomly selected a new search unit within which to systematically search all roads for tracks. We searched for tracks >12 hours after snowfall to ensure that animals had sufficient time to leave tracks throughout the study area. If we found no tracks, we moved

to an adjacent search unit and continued searching. We collected scats along lynx trails for genetic profiling and gender determination by the Wildlife Genetics Laboratory in Missoula, Montana, USA, and we used the results to determine the minimum number of lynx tracked (McKelvey et al. 2006).

We obtained timber-harvest and fire-history maps from 1950 to present from the United States Forest Service Okanogan–Wenatchee National Forest. We classified areas as not harvested or burned from digitized forest stand boundaries, on-site inspections of stand ages, and configurations from 1:40,000 scale orthophotos (United States Department of Agriculture [USDA] Forest Service Pacific Northwest Research Station, Olympia, WA). We developed GIS coverages that contained forest-stand boundaries (i.e., habitat polygons) and identified the forest types and canopy- and understory-cover classes contained in each polygon. We digitized 984 polygons averaging 21 ha ($SD = 48.21$) in size. We classified a forest type for each polygon based on it being comprised primarily of 1) forest opening, 2) recently burned and devoid of forest canopy, 3) Douglas-fir and ponderosa pine forest, or 4) Engelmann spruce and subalpine fir forest. We also classified polygons according to overstory (>2.5 m above the snow) and understory (<2.5 m above the snow) cover classes ($<10\%$, $11\text{--}39\%$, or $40\text{--}100\%$), and slope classes ($0\text{--}30^\circ$ or $31\text{--}76^\circ$). We assigned elevations for polygons into 610–914-m, 915–1,219-m, 1,220–1,524-m, 1,525–1,828-m, or 1,829–2,134-m classes. We used a 10-m resolution digital elevation model (DEM) from the USDA Forest Service, Okanogan–Wenatchee National Forest, and the Spatial Analyst module in ArcMap 8.3 to derive slope and elevation for each polygon.

We ground-truthed 308 polygons and developed a classification-error matrix comparing data from ground-truthed plots with classifications determined from aerial photos, which provided a k coefficient of accuracy for remotely classified polygons (Lillesand et al. 2004). Walker (2005) estimated snowshoe hare densities (hares/ha) in 78 of our habitat polygons based on fecal pellet counts in $3.05\text{-m} \times 5.08\text{-cm}$ plots and the density-estimation model recommended by Krebs et al. (2001).

For habitat analyses, we defined use as a trail segment >600 m long made by one lynx or a presumed female accompanied by kittens. We only used lynx trails >600 m in our analyses; we excluded trails with missing segments due to poor snow-tracking conditions to ensure that each lynx trail transected ≥ 1 polygon. Each trail was continuous and independent. We digitized each trail in the field using a Global Positioning System and recorded locations every 2 seconds or at 1–3-m intervals. We estimated availability of habitats by using GIS to randomly locate a replicate image of each trail in the study area. To minimize Type I error rates, we located the beginning of each availability trail on a road because each use trail began on a road (Katnik and Wielgus 2005). We used 3 replicates of use trails to compile our availability dataset. These replicates represented an asymptote from Monte Carlo simulations of means and

standard deviations for proportions of each vegetative type and physiographic condition recorded along use trails. We considered each trail as our unit of analysis and tallied the sum of lengths for trail segments for each set of use versus availability trails in each forest type and in each canopy cover, understory cover, slope, and elevation class. We estimated proportions by intersecting trails with polygons using GIS (ArcGIS Version 8.3).

We used separate-variance t -tests to determine which variables were useful for distinguishing use versus availability data ($P \leq 0.05$) and would be included as candidate variables in a logistic regression analysis of habitat selection by lynx. We calculated selection ratios (S) for each variable by dividing the mean proportion of use by the mean proportion of availability for each variable (Manly et al. 2002). For selection ratios, we calculated the 95% bootstrap confidence intervals and estimated standard error (Efron and Tibshirani 1993).

We used logistic regression to model relative probability of use by lynx for each variable (McKelvey et al. 2000b, Manly et al. 2002). We considered variables correlated if Spearman's rank correlation coefficient was ≥ 0.50 . We used the collinear variable that had the most significant ($P \leq 0.05$) differences or that we believed was more important to lynx. We included uncorrelated variable sets for all possible combinations of main effects and 2-way interactions in forward stepwise logistic regression. We included variables based on the chi-square improvement statistics and selected the model that yielded the largest log-likelihood chi-square (Manly et al. 2002). The relative probability equation for the logistic regression model was

$$P = \frac{\exp(B_0 + B_1a + B_2b + B_3c \dots)}{1 + \exp(B_0 + B_1a + B_2b + B_3c)}$$

where P is probability of lynx use, B_0 a constant, and B_1a – B_3c parameter coefficients. Our analysis of resource selection was similar to the Design 1 of Manly et al. (2002) with an SP-A protocol, where measurements are made at the population level and units are randomly sampled from both used and available resources. With the exception of 2 small wildfires that burned 0.6% of our study area during summer 2003, distribution of habitat variables did not change during our study.

We used cover classes from the resource-selection model to identify similar attributes for areas where historical lynx records occurred in northern Washington. We recognize that our model only describes habitat selection by lynx during winter and may not include habitat conditions that are important during the denning season or other snow-free periods. We included parameters from the resource-selection model into the Utah State Vegetation Grids (Bio/West Inc 1999) GIS coverage for the area to be inventoried and used the same 10-m DEM to estimate slope and elevation as used to identify selection (see above). We used the lynx habitat model to estimate amount and distribution of suitable lynx habitat in Chelan and western Okanogan counties on the northeastern slope of the

Table 1. Separate variances *t*-tests comparing the proportion of habitat variables for use trails ($n = 51$) obtained by snow-tracking lynx with availability trails ($n = 153$) that we randomly generated using a Geographic Information System in the Black Pine Basin in northern Washington, USA, 2002 to 2004.

Variable	Lynx use trails		Availability trails		<i>t</i> -test	df	<i>P</i> -value	Selection ratios	Selection ratio SE
	\bar{x}	SD	\bar{x}	SD					
Elevation (m)									
610–914	0.006	0.042	0.027	0.120	–1.832	202	0.069	0.220	1.080
915–1,219	0.105	0.293	0.151	0.282	–0.966	83	0.337	0.690	0.216
1,220–1,524	0.449	0.404	0.472	0.395	–0.368	84	0.714	0.950	0.140
1,525–1,828	0.398	0.394	0.319	0.377	1.255	83	0.213	1.250	0.310
1,829–2,134	0.041	0.179	0.030	0.102	0.413	61	0.681	1.360	2.870
Slope (°)									
0–30	0.895	0.114	0.831	0.189	2.888	144	0.004	1.070	0.310
31–76	0.105	0.114	0.169	0.189	–2.888	144	0.004	0.620	0.130
Understory cover (%)									
0–10	0.148	0.190	0.271	0.287	–3.507	131	0.001	0.550	0.100
11–39	0.604	0.291	0.512	0.332	1.876	97	0.064	1.180	0.160
40–100	0.249	0.259	0.217	0.252	0.772	84	0.442	1.150	0.190
Canopy cover (%)									
0–10	0.175	0.193	0.281	0.293	–2.948	131	0.004	0.620	0.090
11–39	0.481	0.301	0.373	0.292	2.248	84	0.027	1.290	0.100
40–100	0.343	0.283	0.345	0.286	–0.051	86	0.959	0.990	0.230
Vegetation types									
Recent burn (<10 yr)	0.045	0.115	0.118	0.277	–2.643	193	0.009	0.380	0.100
Forest openings	0.005	0.016	0.018	0.070	–2.079	190	0.039	0.270	0.200
Douglas fir–ponderosa pine	0.137	0.220	0.333	0.351	–4.662	139	<0.01	0.410	0.110
Engelmann spruce–subalpine fir	0.813	0.241	0.532	0.371	6.228	133	<0.01	1.528	0.120

Cascade Range, where presence of lynx have been documented in the past decade, and in the remaining northern counties where lynx occurred historically but not consistently during the past decade. We used Koehler's (1990) estimate of 2.3 lynx/100 km² for the Meadows during 1985–1987 to estimate numbers of lynx that may occupy these habitats.

RESULTS

We used data from 51 lynx trails and 153 random trails for analysis of selection patterns, including 19 trails obtained during winter of 2002–2003 and 32 trails obtained during 2003–2004. Mean length of lynx trails for winters 2002–2003 and 2003–2004 was 2,591 m (SD \pm 1,495) and 3,138 m (\pm 1,296), respectively. Our sample represents trails from ≥ 9 unique lynx, 6 males and 3 females (B. T. Maletzke, Washington State University, unpublished data). Some of these samples may have been from kittens accompanying their mothers because trails were sometimes composed of multiple tracks.

When we compared habitat data from 308 ground-truthed plots with classifications determined from aerial photos, the classification-error matrix showed a high overall accuracy of 86% for remotely classified polygons. The \hat{k} coefficient was 0.75 (75% better than random; Lillesand et al. 2004). The understory coverage had an overall accuracy of 60% (\hat{k} = 0.37), and the 3 overstory canopy-cover classes had 68% accuracy (\hat{k} = 0.52).

Lynx used Engelmann spruce and subalpine fir forests with moderate canopy and understory cover (11–39%) and flat to moderate slopes ($\leq 30^\circ$) more than expected (Table 1) and Douglas-fir and ponderosa pine forest, forest openings,

and recently burned areas with sparse canopy and understory cover (<10%), low elevations (<915 m), and steep slopes ($\geq 30^\circ$) less than expected (Table 1). We found no evidence of selection for or against high canopy and understory cover (>40%).

We included forest type, canopy cover, understory cover, elevation, and slope in the logistic regression analyses (Table 1). Engelmann spruce and subalpine fir forest, moderate canopy cover, relatively high elevations (1,525–1,828 m), and flat to moderate slopes ($< 30^\circ$) were included in the best-fit model (Table 2). Because moderate understory cover was correlated with moderate canopy cover (Spearman's ρ = 0.31, r^2 = 0.62), forest type (Spearman's ρ = 0.356, r^2 = 0.71), and elevation (Spearman's ρ = 0.13, r^2 = 0.26), we did not include it in the final model.

Selection for Engelmann spruce and subalpine fir forest, moderate canopy cover, flat to moderate slopes, and relatively high elevations was reflected in the large positive parameter coefficients, and avoidance of Douglas-fir and ponderosa pine forest, forest openings, recent burns, sparse canopy and understory cover, and relatively steep slopes was reflected in the large negative constant (Table 3). Probability of use by lynx was 19.4 times greater in Engelmann spruce and subalpine fir forest than in other vegetation types, 4.9 times greater in areas with moderate canopy cover than for other cover classes, 5.0 times greater at elevations ranging from 1,525 m to 1,829 m than at other elevations, and 48.8 times greater on flat to moderate slopes than on steep slopes. The model shows a good fit to the data (likelihood ratio χ^2 = 43.447, df = 4, P < 0.01, McFadden's ρ^2 = 0.19; Hensher and Johnson 1981, Steinberg and Colla 2000).

Based on these selection patterns, we mapped Engelmann

Table 2. Process of model selection for logistic regression analyses of landscape-scale habitat selection by lynx in the Black Pine Basin in northern Washington, USA, 2002 to 2004.

Model variables	Likelihood ratio			Improvement			ρ^{2a}
	χ^2	df	P-value	χ^2	df	P-value	
Engelmann spruce–subalpine fir	26.310	1	0.000				0.12
Engelmann spruce–subalpine fir, slope 0–30°	30.852	2	0.000	4.542	1	0.03	0.13
Engelmann spruce–subalpine fir, slope 0–30°, elevation 1,525–1,828 m	37.011	3	0.000	6.159	1	0.01	0.16
Engelmann spruce–subalpine fir, slope 0–30°, elevation 1,525–1,828 m, canopy 11–39% ^b	43.447	4	0.000	6.436	1	0.01	0.19
Engelmann spruce–subalpine fir, slope 0–30°, elevation 1,525–1,828 m, canopy 11–39%, understory 0–10%	45.050	5	0.000	1.603	1	0.21	0.20
Engelmann spruce–subalpine fir, slope 0–30°, elevation 1,525–1,828 m, canopy 11–39%, canopy \times elevation	45.105	5	0.000	1.658	1	0.20	0.20

^a McFaddens's ρ^2 .

^b Model with the best fit; $P = \frac{\exp[-7.792+2.967(\text{ESSF})+3.888(\text{slope} < 30)+1.601(\text{elev} 1,525-1,828\text{m})+1.594(\text{canopy} 11-39\%)]}{1+\exp[-7.792+2.967(\text{ESSF})+3.888(\text{slope} < 30)+1.601(\text{elev} 1,525-1,828\text{m})+1.594(\text{canopy} 11-39\%)]}$.

spruce and subalpine fir forests, moderate canopy cover, flat to moderate slopes, and elevations ranging from 1,525 m to 1,829 m using the Utah State Vegetation Grids GIS coverage and the 10-m DEM and estimate 2,411 km² of suitable lynx habitat for Chelan and western Okanogan counties and 1,381 km² of habitat in the remaining northern counties (Fig. 1). Based on Koehler's (1990) estimate of 2.3 lynx/100 km², we estimate that Washington is capable of supporting approximately 87 lynx.

DISCUSSION

During winter in the Black Pine Basin, lynx selected forests dominated by Engelmann spruce and subalpine fir, with moderate canopy cover occurring on flat to moderate slopes at relatively high elevations. Although only 55% of our study area consisted of Engelmann spruce and subalpine fir forest, 81% of the distance of lynx trails occurred in those types. These are similar to selection patterns reported for lynx in the Meadows study area, 16 km east of the Black Pine Basin, where lynx selected for lodgepole pine forests, which is a seral stage of Engelmann spruce and subalpine fir climax forest and the dominant cover type there (Koehler 1990, McKelvey et al. 2000b, von Kienast 2003).

Lynx may select areas with moderate canopy cover because it permits understory growth that provides security cover and forage for snowshoe hares (Fuller et al. 2007), the preferred prey of lynx in Washington and elsewhere (Koehler 1990, Aubry et al. 2000, Mowat et al. 2000, von

Kienast 2003, Maletzke et al. 2008). Lynx avoided forest openings, burned areas, and other areas in the Black Pine Basin where canopy cover was <10%, as has been reported elsewhere (Koehler 1990, Murray et al. 1994). von Kienast (2003) did not encounter lynx tracks in the 1994 Thunder Mountain burn (42 km²) in the Meadows study area and did not observe lynx crossing openings >150 m in width. However, we documented lynx crossing burned areas in the Black Pine Basin to access unburned patches where densities of snowshoe hares were high (Walker 2005). Lynx avoided Douglas-fir and ponderosa pine stands, where snowshoe hares densities were lower than in Engelmann spruce and subalpine fir forests (Koehler 1990, Walker 2005).

Engelmann spruce, subalpine fir, and seral lodgepole pine forests supported high densities of hares and were used by lynx for foraging during winter (Koehler 1990, Walker 2005, Maletzke et al. 2008). Hare densities were higher where these stand types were more contiguous, such as in the Meadows ($\bar{x} = 1.3 \pm 0.1$ hares/ha, $n = 26$), than in the more fragmented forests of the Black Pine Basin ($\bar{x} = 0.9 \pm 0.1$ hares/ha, $n = 78$; Walker 2005). Although they may not accurately estimate hare densities, we believe pellet counts provided reliable comparisons of relative abundance between these nearby study areas (Mills et al. 2005).

Elevations occupied by lynx in the Black Pine Basin were similar to elevations occupied by lynx in the Meadows study area (1,400–2,000 m; Koehler 1990, McKelvey et al. 2000b, von Kienast 2003). Selection for moderate slopes by lynx has

Table 3. Logistic regression model distinguishing lynx use trails (response = 1) from availability trails (response = 0) in the Black Pine Basin in northern Washington, USA, 2002 to 2004.

Variables ^a	B	SE (B)	T-ratio	P-value	Odds ratio ^b
Engelmann spruce–subalpine fir ^c	2.967	0.676	4.386	<0.01	19.424
Slope 0–30°	3.888	1.386	2.805	0.01	48.822
Elevation 1,524–1,828 m	1.601	0.566	2.827	0.01	4.956
Canopy cover 11–39% ^d	1.561	0.642	2.479	0.01	4.924
Constant	−7.792	1.584	−4.919	<0.01	

^a Wald Statistic for each of the habitat variables was significant at $P < 0.05$, $-2 \log \text{likelihood} = 185.986$, model $\chi^2 = 43.447$, $df = 4$, $P < 0.001$.

^b Odds ratio = $\exp(\beta)$; the factor by which the odds that an area will be used by lynx change for every unit increase in the independent variable.

^c Forest containing lodgepole pine, Engelmann spruce, or subalpine fir.

^d Canopy cover estimated >2.5 m above snow surface or through aerial photo interpretation.

also been reported in other southern boreal forests (Apps 2000, McKelvey et al. 2000b, von Kienast 2003).

We used habitat features that were selected by lynx in this study, and considered important in other study areas, to identify habitat conditions that may support lynx elsewhere in northern Washington. We believe this was a valid application of the model because the Black Pine Basin contained fragmented habitats that were similar to those occurring throughout northeastern Washington. In addition, the Black Pine Basin and Meadows areas supported the only reproducing lynx populations in Washington, based on observations of the tracks of females with kittens since the 1980s; thus, we hypothesized that similar habitat conditions elsewhere in Washington could also support lynx (Koehler 1990, von Kienast 2003, Maletzke 2004).

Based on estimates of approximately 3,800 km² of suitable lynx habitat in the northern counties (Fig. 1), Washington may support approximately 87 lynx. However, this may be an overestimate because it is based on estimated lynx densities in an area where hare densities were high, and where favorable habitat conditions for lynx were more contiguous than elsewhere in the state (Walker 2005).

Lynx were likely more widespread and abundant in northern Washington during the 1960s and 1970s, because >57 lynx were trapped during this period (Stinson 2001). Snow-tracking surveys by agency and volunteer personnel since 1990 documented lynx intermittently in northeastern Washington, but consistently in western Okanogan County, where resident populations were known to occur based on continuous evidence of their presence and observations of kitten tracks during winter each year that surveys were conducted (Stinson 2001; D. W. Stinson, Washington Department of Fish and Wildlife, unpublished data).

Mapped habitat for lynx in Washington was often contained in insular or peninsular stands of Engelmann spruce, subalpine fir, or lodgepole pine (Fig. 1), similar to that found in the Black Pine Basin, where shrub-steppe communities at lower elevations, and alpine meadows and barren rock at higher elevations, bound habitats. Douglas-fir and ponderosa pine forests on southerly aspects, which are avoided by lynx, further fragment these habitats. Wildfires and timber-harvest activities have influenced lynx habitat temporally as well. Fires are a significant disturbance process in boreal forests of North America, and large areas burned throughout Washington during the 19th and 20th centuries (Agee 2000). In the past 2 decades, >50% of the 2,411 km² of suitable habitat for lynx in Chelan and Okanogan counties have burned, including the 600-km² Tripod Fire that burned most of the Meadows study area in 2006 (Fig. 1), which was considered the best and most extensive lynx habitat in Washington (Stinson 2001).

Annual snow-tracking surveys indicate that lynx may occasionally immigrate into other counties that border British Columbia. Although habitat for lynx is more sparsely distributed in these counties than was present in Okanogan County prior to the Tripod Fire (Fig. 1), between 400 km² (our model) and 987 km² (Stinson 2001) of suitable lynx

habitat may be present in the Kettle Range in Ferry County. Thus, this area may be capable of supporting 10–23 lynx, based on a predicted density of 2.3 lynx/100 km² (Koehler 1990). Trapping records indicate that the Kettle Range supported a population of lynx during the 1960s and 1970s (Stinson 2001). We suspect that over-trapping resulted in the extirpation of lynx from this isolated mountain range 30 years ago. The Kettle Range is a montane island surrounded by low-elevation plant communities dominated by shrub-steppe and Douglas-fir and ponderosa pine forests, which are avoided by lynx. In addition, a fence at the northern end of the Kettle Range in British Columbia, designed to prevent vehicle collisions with bighorn sheep (*Ovis canadensis*) and deer (*Odocoileus* sp.) in a major highway corridor, may have created a barrier for lynx dispersal and recolonization in this portion of their former range in Washington.

MANAGEMENT IMPLICATIONS

Our habitat model predicts there is habitat adequate to support 10–23 lynx in the Kettle Range. However, we believe the probability of lynx recolonizing the Kettle Range from British Columbia is low and recommend that a feasibility assessment be conducted on the reintroduction of lynx, as was recently done for the potential reintroduction of fishers (*Martes pennanti*) in Washington (Lewis and Hayes 2004). A genetic evaluation of potential source populations is needed if reintroduction is to be considered. Our habitat model in conjunction with our knowledge of lynx hunting behavior and foraging habitats can help identify the scale and distribution of potential foraging habitats for lynx. The assessment will require surveys to obtain reliable estimates of snowshoe hare densities in various habitat conditions. If the prey base is considered adequate, reintroducing lynx to the Kettle Range may be an appropriate conservation strategy.

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LITERATURE CITED

- Agee, J. K. 2000. Disturbance ecology of North American boreal forests and associated Northern mixed/subalpine forests. Pages 39–82 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.
- Apps, C. D. 2000. Space-use, diet, demographics, and topographic

- associations of lynx in the southern Canadian Rocky Mountains: a study. Pages 351–371 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.
- Aubry, K. B., G. M. Koehler, and J. R. Squires. 2000. Ecology of Canada lynx in southern boreal forests. Pages 373–396 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.
- Bio/West Inc. 1999. Vegetation mapping on the Okanogan and Colville National Forests using Landsat Thematic Mapper images. Bio/West, Logan, Utah, USA.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, USA.
- Fuller, A. K., D. J. Harrison, and J. H. Vashon. 2007. Winter habitat selection by Canada lynx in Maine: prey abundance or accessibility? *Journal of Wildlife Management* 71:1980–1986.
- Hensher, D., and L. W. Johnson. 1981. Applied discrete choice modeling. John Wiley and Sons, New York, New York, USA.
- Katnik, D. D., and R. B. Wielgus. 2005. Landscape proportions versus Monte Carlo simulated home ranges for estimating resource availability. *Journal of Wildlife Management* 60:20–32.
- Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Canadian Journal of Zoology* 68:845–851.
- Krebs, C. J., R. Boonstra, V. Nams, M. O'Donoghue, K. E. Hodges, and S. Boutin. 2001. Estimation of snowshoe hare population density from pellet plots—a further evaluation. *Canadian Journal of Zoology* 79:1–4.
- Lewis, J. C., and G. E. Hayes. 2004. Feasibility assessment for reintroducing fishers to Washington. Washington Department of Fish and Wildlife, Olympia, USA.
- Lillesand, T. M., R. W. Kiefer, and J. W. Chipman. 2004. Remote sensing & image interpretation. Fifth edition. John Wiley and Sons, New York, New York, USA.
- Maletzke, B. T. 2004. Winter habitat selection of lynx (*Lynx canadensis*) in northern Washington. Thesis, Washington State University, Pullman, USA.
- Maletzke, B. T., G. M. Koehler, R. B. Wielgus, K. B. Aubry, and M. A. Evans. 2008. Habitat conditions associated with lynx hunting behavior during winter in northern Washington. *Journal of Wildlife Management* 72:1473–1478.
- Manly, B. F., J. L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Boston, Massachusetts, USA.
- McKelvey, K. S., K. B. Aubry, and Y. K. Ortega. 2000a. History and distribution of lynx in the contiguous United States. Pages 207–259 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.
- McKelvey, K. S., Y. K. Ortega, G. M. Koehler, K. B. Aubry, and J. D. Brittell. 2000b. Canada lynx habitat and topographic use patterns in north central Washington: a reanalysis. Pages 307–336 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.
- McKelvey, K. S., J. A. von Kienast, K. B. Aubry, G. M. Koehler, B. T. Maletzke, J. R. Squires, E. L. Lindquist, S. Loch, and M. K. Schwartz. 2006. DNA analysis of hair and scats collected along snow tracks to document the presence of Canada lynx. *Wildlife Society Bulletin* 34:451–455.
- Mills, L. S., P. G. Griffin, K. E. Hodges, K. McKelvey, L. Ruggiero, and T. Ulizio. 2005. Pellet count indices compared to mark–recapture estimates for evaluating snowshoe hare density. *Journal of Wildlife Management* 69:1053–1062.
- Mowat, G., K. G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in Northern Canada and Alaska. Pages 265–306 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.
- Murray, D., L. S. Boutin, and M. O'Donoghue. 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. *Canadian Journal of Zoology* 71:1444–1451.
- Steinberg, D., and P. Colla. 2000. Logistic regression. Pages 549–613 in Systat 10 Statistics I. SPSS Inc., Chicago, Illinois, USA.
- Stinson, D. W. 2001. Washington state recovery plan for the lynx. Washington Department of Fish and Wildlife, Olympia, USA.
- U.S. Fish and Wildlife Service. 2000. Determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule; final rule. *Federal Register* 65:16051–16086.
- von Kienast, J. A. 2003. Winter habitat selection and food habits of lynx on the Okanogan Plateau, Washington. Thesis, University of Washington, Seattle, USA.
- Walker, C. J. 2005. Influences of landscape structure on snowshoe hare populations in fragmented forests. Thesis, University of Montana, Missoula, USA.
- Washington Department of Wildlife. 1993. Status of the North American lynx (*Lynx canadensis*) in Washington. Washington Department of Wildlife, Olympia, USA.

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